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Eurya stigmosa (Theaceae), a new and extinct record for the Calabrian stage of Madeira Island (Portugal): $^{40}Ar/^{39}Ar$ dating, palaeoecological and oceanic island palaeobiogeographical implications

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ABSTRACT

The general dynamic model of oceanic island biogeography (GDM) predicts the immigration, speciation and extinction of terrestrial biota through geological time on oceanic islands. Additionally, the glacial-sensitive model of island biogeography (GSM) also predicts extinction due to eustatic and climate change within islands. However, well-documented and natural pre-Holocene plant extinctions are almost unknown for oceanic islands worldwide. To test these predictions, we have sampled the Early Pleistocene Porto da Cruz lacustrine and fluvial sediments for plant fossils that could confirm the GDM and GSM extinction predictions. Additionally, two new $^{40}Ar/^{39}Ar$ geochronological analyses were performed, constraining the age of the sediments to 1.3 Ma (Calabrian). Among the fossils, *Eurya stigmosa* (R.Ludw.) Mai (Theaceae) seeds were recognised and studied by scanning electron microscopy (SEM). *E. stigmosa* is the first report of a natural (non-anthropogenic) extinct plant in the fossil record for Madeira Island, and for an oceanic island, confirming the GDM and GSM predictions. *Eurya* spp. palaeobiogeography indicates wider distribution in Europe until the end of the Pliocene (2.58 Ma), becoming extirpated to small refugia and extinct thereafter. The Madeiran record expands the formerly unknown presence of *E. stigmosa* to the Macaronesian realm. The new dating of the deposit at 1.3 Ma (Calabrian) means that *E. stigmosa* in Madeira was already in a refugium. The extinction in Madeira is most probably a combination of island ontogeny and climate change due to Pleistocene glaciations. The palaeoecological role of this extinct shrub or tree is currently unknown, but it was a probably an element of the Madeiran laurel forest, as this community was already present in Madeira at least 1.8 My ago. This new information corroborates the predictive power of GDM and GSM and adds a new view on the importance of studying oceanic island palaeobotany, specially palaeocarpofloras.

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1. Introduction

Oceanic Islands natural laboratories' paradigm is more active than it has ever been (e.g. Whittaker and Fernández-Palacios, 2007; Whittaker et al., 2017). At the present day, oceanic islands are unequivocal places to answer neontological questions focused on biogeographical, evolutionary and ecological problems (e.g. Whittaker and Fernández-Palacios, 2007; Fernández-Palacios et al., 2015; Warren et al., 2015; Patiño et al., 2017).

The recent development of the general dynamic model of

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oceanic island biogeography (GDM) (Whittaker et al., 2007, 2008; Borregaard et al., 2016) allows us to understand how geological dynamics of oceanic islands affected the terrestrial biota on a geological scale (ky to My). If we focus in three GDM theorical components, the immigration, speciation and extinction (or extirpation) theoretical curves, today we can empirically pinpoint the emigration and speciation end result (i.e. observed neoendemic and palaeoendemic taxa), but past extinctions are elusive, as already pointed out by Whittaker et al. (2008) when describing the final stages of island ontogeny: '*Evidence for the loss of species as a result of island erosion and subsidence (…) … is likely to be extremely hard to demonstrate unequivocally as the likelihood of finding fossil evidence is negligible in such circumstances.*' (Whittaker et al., 2008, pp. 989).

As proposed by the GDM, the geological ontogeny of oceanic islands, such as volcanism and erosion during quiescence periods, are the key taphonomical processes where island biota can be preserved as fossils (e.g. Spicer, 1989; Góis-Marques et al., in press). Recent palaeozoological studies (e.g. Olson and James, 1982; Alcover et al., 2015; Rando et al., 2017) demonstrate the presence of fossils of endemic extinct birds, but these are relatively geologically young (Late Pleistocene to Holocene), and their loss explained by anthropogenic impacts (see Wood et al., 2017).

Recently, Fernández-Palacios et al. (2015) developed a glacial-sensitive model of island biogeography (GSM), proposing that oceanic islands extinctions would be the result of Pleistocene glaciations. One of the predictions was that "*Palaeontological and palaeoecological research will make clear that several natural extinctions, caused by area reduction following sea level transgressions, occurred before human arrival to oceanic islands*" (Fernández-Palacios et al., 2016, in box 1, pp. 820).

Palaeobotanical and palynological studies (especially in a palaeoecological context) on oceanic islands that explore terrestrial sediments and volcanic terrestrial deposits reveal that plant microfossils (e.g. de Nascimento et al., 2009; de Boer et al., 2013; Cañellas-Boltà et al., 2016; Rull et al., 2017) and plant macrofossils (e.g. Anderson et al., 2009; Góis-Marques and Menezes de Sequeira, 2015; Góis-Marques et al., 2018; Góis-Marques et al., in press) are present and abundant.

Importantly, these palaeofloras can have a geological span of millions of years within the same archipelago, as found for Canary archipelago palaeofloras, where macrofossil data (e.g. leaves) and microfossils (pollen and spores) span from Miocene (13 Ma; García-Talavera et al., 1995) to Late Holocene (e.g. de Nascimento et al., 2015), with several other paleofloras reported of intermediate ages (Anderson et al., 2009, and references therein). But although there is an abundant plant fossil record spanning from recent to several millions of years, there is no record so far of extinct plants, leading to the question: where are the extinct plants in the fossil record of oceanic islands, as predicted by the extinction curve of the GDM and the GSM?

As previous works refer (Góis-Marques, 2013; Góis-Marques et al., 2014, 2018), Madeira Island (mid-Atlantic Ocean) is a potential test location for these biogeographical and palaeobotanical questions. Madeira has been explored since the mid-19th century (Lyell, 1854, 1855; Heer, 1857; Bunbury, 1859; Hartung and Mayer, 1864) for plant fossils. Recent efforts have been undertaken to revise previously collected material, and identify and collect new, complementary specimens (Góis-Marques, 2013; Góis-Marques et al., 2014, 2018). One of the productive fossil beds is located in northeast Madeira Island at Porto da Cruz. This site was discovered in 1859 by James Yate Johnson (1820–1900) and a small palaeoflora described by Hartung and Mayer (1864). Recent reinvestigation of this fossil locality revealed the presence of abundant carpological (seeds and fruits) fossils.

In this paper, we aim to accurately date the Porto da Cruz sediments through new $^{40}Ar/^{39}Ar$ geochronology which will provide a conclusive date for the fossils. Additionally, we will describe the first extinct oceanic island plant from well-preserved fossils, discuss the implications for oceanic island palaeobiogeography within the frame of the GDM and GSM, and finally debate the palaeoecological implications.

2. Extinct fossil plants in oceanic islands: where are they?

In this section we will use the terms 'extinction' (meaning a global loss) and 'extirpation' (meaning local loss but found elsewhere) as defined by Whittaker and Fernández-Palacios (2007).

Evidence of natural (non-anthropogenic) extinctions from fossils of vascular plants (i.e. Pteridophyta and Spermatophyta) on oceanic islands are illusive. The literature shows that plant macrofossils exist on several oceanic islands, such as Hawaii (e.g. Lyon, 1930; Walker, 1995; Woodcock and Kalodimos, 2005; Woodcock and Maekawa, 2006), Marianas (Fosberg and Corwin, 1958), Galápagos (e.g. Coffey et al., 2011), Marquesas (Plessis et al., 1978), Tristan da Cunha (e.g. Preece et al., 1986), Azores (Góis-Marques et al., in press, and references therein), Madeira (e.g. Heer, 1857; Bunbury, 1859; Góis-Marques et al., 2018), Canaries (e.g. Schmincke, 1968; García-Talavera et al., 1995; Vegas Salamanca et al., 1998; Anderson et al., 2009; Marrero, 2013; Suárez-Rodrígues, 2013), and Cabo Verde (Chevalier et al., 1935). Plant fossils are also known from subsided islands in the Indian Ocean (Carpenter et al., 2010). However, these papers mainly report the existence of fossils or use them to assess the native status of plant species. One exception is Fosberg (1977) that describes a new extinct species, *Garcinia laddii* Fosberg (Clusiaceae), based on fruit fossils found within Late Pleistocene (~25 ka) marine sediments from Espiritu Santo Island, Vanuatu (South Pacific Ocean). Later, Kostermans (1982) wrote an opinion that *G. laddii* fruit fossils fit better within the genus *Diospyrus* L. (Ebenaceae), proposing the combination *Diospyrus laddii* (Fosb.) Kosterm. This new nomenclatural combination was published without the analysis of the specimens. Further studies are needed to understand if these fruit fossils belong to an extinct taxon.

So far, Macaronesian archipelagos are the best explored, with several publications on their palaeobotany and palynology in palaeoecological reconstructions. In Madeira Island, Heer (1857) was the first to suggest the existence of extinct and extirpated European plants (e.g. *Ulmus* L., *Corylus* L.) from the São Jorge leaf-bed. However, this macroflora was described to fit the old Atlantis theory. A recent review of the surviving specimens (Góis-Marques et al., 2018), demonstrated that São Jorge palaeoflora is composed mainly by native plants (e.g. *Corylus* leaf fossils were reviewed as *Rubus* sp.), although some unidentified morphotypes (due to poor preservation) could correspond to extinct or extirpated taxa. In the Canary Islands, some recent reports also shed light into extinct and extirpated plant taxa; Anderson et al. (2009) reports the extirpation on Gran Canaria for the Pliocene of cf. *Tetraclinis,* although a detailed palaeobotanical study is needed to confirm this identification. Another Pliocene macroflora from Gran Canaria is described by Marrero (2013), where they suggest that most of this flora seems to be extinct. However, the poor preservation of the material prevented the author from describing new or extinct taxa. The only attempt to describe an extinct plant fossil from the Canary Islands is the species *Dracaenites roquenubli* C.Suárez (2.7–5.5 My), based on gross morphology of fragmentary leaf specimens (Suárez-Rodrígues, 2013). However, further fossil material and micromorphological studies are needed to confirm if this taxon is separate from *Dracaena* (a native to the Canary Islands) or not. As a remark, recent work by Denk et al. (2014) clearly shows

the existence of *Dracaena (D. tayfunii* Denk, H.T.Güner, G.W.Grimm) in Anatolia 16 My ago (Miocene). It is worth mentioning that in Tenerife, although most probably related to anthropogenic extinctions, an unexpected result shows the presence of *Carpinus* sp. and *Quercus* sp. fossil pollen (de Nascimento et al., 2009). However, currently it is not possible to validate if these correspond to extinct or extirpated species.

Natural worldwide oceanic island extinctions in the fossil record are seldom documented or poorly supported. Most can be explained by taxa extirpations or are based on specimens that need further taxonomical studies to confirm their systematic position, and consequently their extirpation/extinction status on those islands.

3. Geological setting

3.1. Madeira Island

Madeira Island is located in the central Atlantic Ocean (Fig. 1A), at *ca*. 700 km west of the north-west coast of Morocco (Africa) and *ca*. 850 km south-west of mainland Portugal (Europe). The island is part of the Madeira Archipelago composed of the islands Madeira (the largest island with 736 km^2, reaching 1861 m a.s.l.) and Porto Santo (43 km^2; 517 m a.s.l.), and by the islets of Desertas (14 km^2, 442 m a.s.l.) and Selvagens (4 km^2, 163 m a.s.l.).

Madeira Island (Fig. 1B) is an intensely dissected shield volcano of Miocene (>7 Ma; Ramalho et al., 2015) to Holocene age (last dated volcanism 6–7 ka; Geldmacher et al., 2000) that sits on the NW sector of the Nubian plate (Fig. 1A). In this geodynamic setting, the intra-plate volcanism is commonly explained by a hotspot trending NNE-SSW from south mainland Portugal to the Madeira archipelago (Gorringe, Ampere and Coral Patch, Unicorn, Seine, Porto Santo and Madeira; Geldmacher et al., 2005). Furthermore, Brum da Silveira et al. (2010a) suggest that a volcano-tectonic interaction between the mantle plume and a set of WNW-ESE to EW trending structures could have contributed to building Madeira Island.

According to Brum da Silveira et al. (2010a, b, c) Madeira Island was constructed by three major eruptive events recorded as three volcanic complexes and their respective volcano-stratigraphic units. The oldest is the Lower Volcanic Complex (LVC) that corresponds to submarine (LVC1: Porto da Cruz unit) and emergent (LVC2: Lameiros unit) phases (>7.0 Ma; Ramalho et al., 2015), the Middle Volcanic Complex (MVC) corresponding to the sub-aerial shield-volcano building (MVC1: Encumeada unit; MVC2: Penha d'Águia unit; MVC3: Curral das Freiras unit) between 7.0 and 1.8 Ma, and the Upper Volcanic Complex (UVC) corresponding to capping (UVC1: Lombos unit) and post-erosional (UVC2: Funchal unit) volcanism, developed since 1.8 Ma to late Holocene. All volcanic complexes are associated with interlayered sedimentary deposits, specially debris flows or mud flows (lahars), and hyperconcentrated flows (Brum da Silveira et al., 2010a).

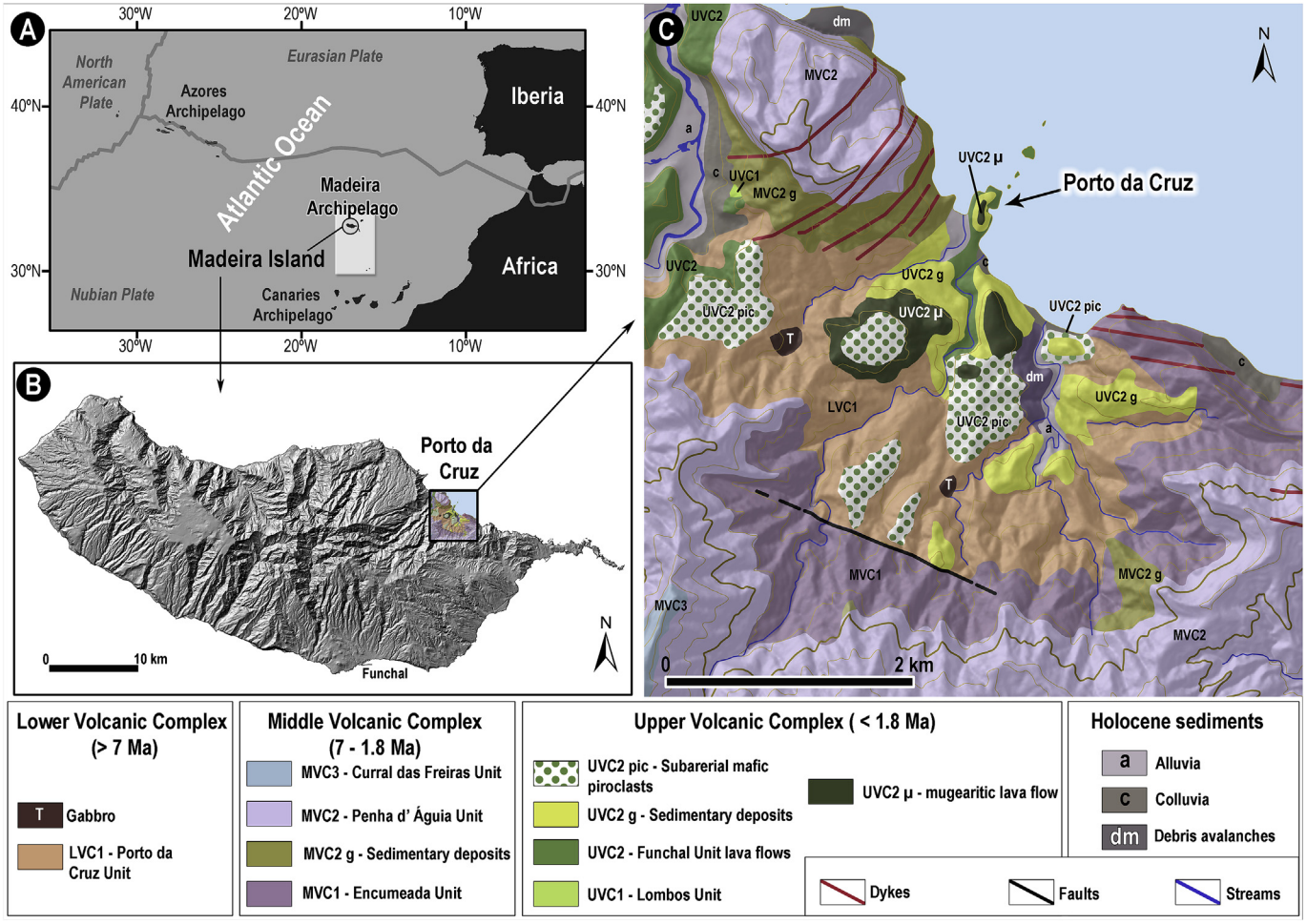

Fig. 1. Geographical location of Madeira Island and the Porto da Cruz sediments (UVC2 g). **A**, Location and geodynamic setting of Madeira Archipelago; **B**, digital elevation model of Madeira island with the Porto da Cruz location; **C**, geological map of the Porto da Cruz area adapted from Brum da Silveira et al. (2010b).

3.2. Porto da Cruz sediments

According to Brum da Silveira et al. (2010a), the Porto da Cruz area exposes the oldest rocks from the LVC and MVC that were covered by younger volcanism and sediments from the UVC (Fig. 1C). The geological map (Brum da Silveira et al., 2010b, Fig. 1C) shows that LVC1, MVC 1 and 2 occupy most of the Porto da Cruz area. These volcanic complexes were exposed by a landslide (Geldmacher et al., 2000; Quartau et al., 2018) and were fluvially eroded at least until the initial phase of UVC 2 (Fig. 1C). The valleys formed were then filled by lava flows from the UVC2, fluvial sediments (UVC2 g), and covered by a mugearitic lava flow (UVC2 μ; Fig 1C; 2B). The sediment accumulation is most likely explained by flood deposits inside fluvial valleys naturally dammed by landslides or lava flows (Brum da Silveira et al., 2010a).

The Porto da Cruz sedimentary sequence is best exposed in the sea cliffs of the promontory of that village (NE sector; Fig. 1A). The sedimentary sequence is composed mainly of fluvial conglomerates, sandstones, siltstones and rare mudstone layers. At the base of the sequence (layer 2; Fig. 2B) a palaeosol is present, associated with adpressions and compressions of plant macro and mesofossils (Góis-Marques, 2013). The overlying mugearitic lava flow, UVC2 μ was dated by K–Ar by Mata (1996), yielding an age of 1.5 Ma. This allowed the restriction of the sedimentary deposit to an age of 1.8 Ma (upper age of the UVC) to 1.5 Ma (Góis-Marques, 2013). The underlying basaltic lava flow (*s.l*) UVC 2 wasn't dated until now.

4. Material and methods

4.1. Geochronology

4.1.1. Field sampling

To constrain the age of the sediments, the lava flows underlying and overlying the sedimentary sequence were sampled for $^{40}Ar/^{39}Ar$ geochronologic dating. The overlying mugearitic lava flow (UCV2 μ) sample nº 1, was collected at 32º46′32.0″ N, 16º49′37.8″ W; the underlying basaltic lava flow (UCV2), sample nº 2, was collected at 32º46′33.7″N, 16º49′38.8″W. Sampling was performed according to the recommendations by Chisholm et al. (2014).

4.1.2. $^{40}Ar/^{39}Ar$ analysis

After removing the outer part of each sample, two crushate were obtained (>250 mg each) and sent to the Ar/Ar and Noble Gas

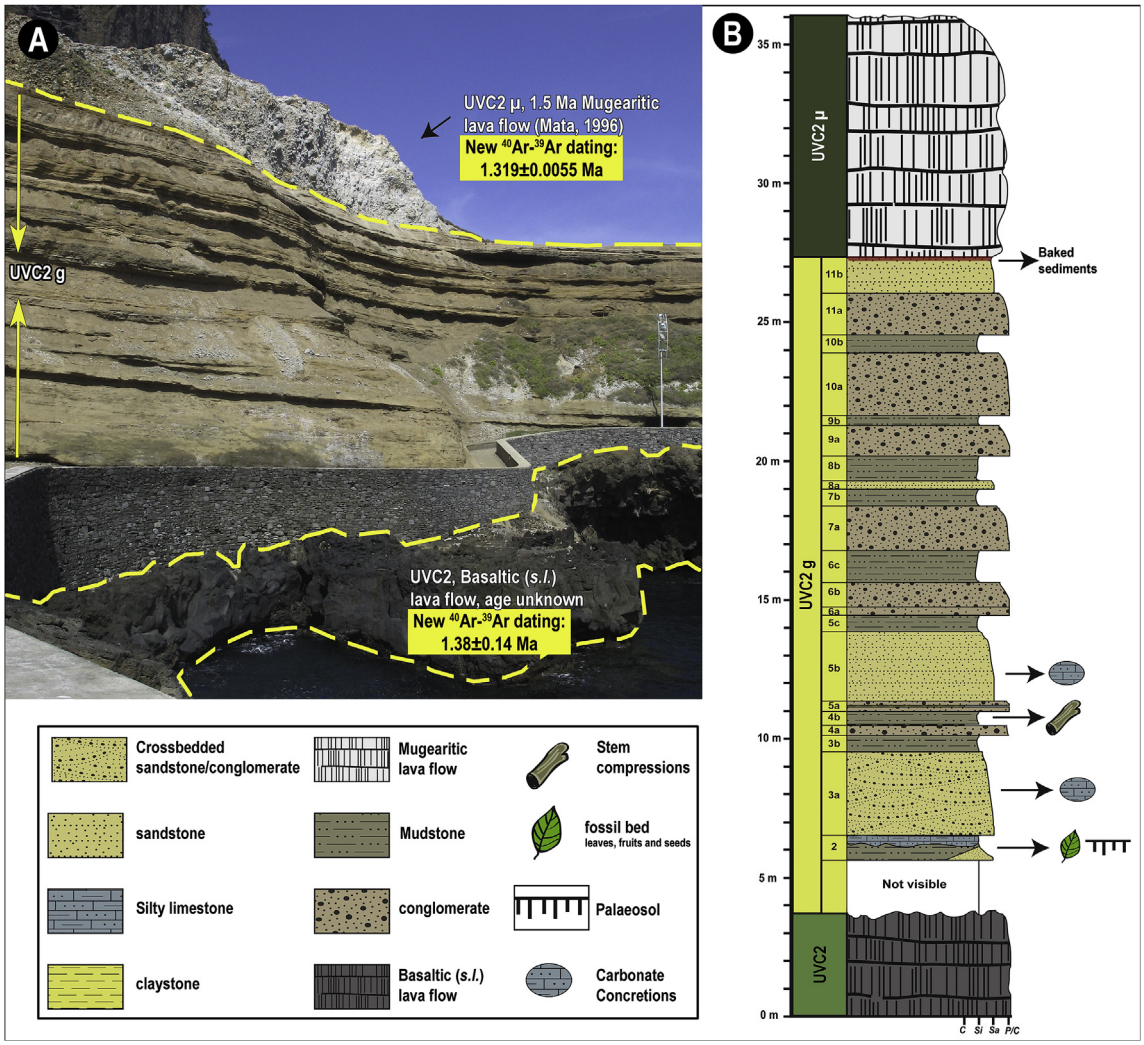

Fig. 2. Stratigraphy of the Porto da Cruz sedimentary deposit. **A,** overview of the eastern face of the promontory and the sampling sites for $^{40}Ar/^{39}Ar$ dating for the overlying (UVC2 μ) and underlying (UVC2) lava flows. **B**, lithostratigraphic column of the East section of the promontory of Porto da Cruz, adapted from Góis-Marques (2013). Horizontal axis **C**-clay; **Si**– silt; **Sa**-Sand; **P/C**- Pebbles and cobbles.

Research Laboratory, at The Open University, UK.

The $^{40}Ar/^{39}Ar$ dating protocol follows Su et al. (2018), with minor modifications. The samples were further crushed and washed with de-ionised water. Under a stereoscope, unaltered rock samples were chosen, and cleaned with acetone, de-ionised water, and were ultrasonically cleaned. Samples were irradiated in the McMaster Nuclear Reactor (McMaster University, Canada) for 4 h using Cadmium shielding. Samples were held in position 8D. The neutron flux was monitored using biotite mineral standard GA1550 which has an age of 99.738 ± 0.104 Ma (Renne et al., 2011). The Standards were packed for irradiation on either side of the unknown samples and analysed using the single grain fusion method using a 1059 nm CSI fibre laser and a MAP215-50 mass spectrometer. The J values were calculated by linear extrapolation between the two measured J values.

The irradiated samples were loaded into an ultra-high vacuum system, and a 1059 nm CSI fibre laser was focussed into the sample chamber and used to step-heat the samples. After passing through a liquid nitrogen trap, extracted gases were cleaned for 5 min using 3 SAES AP-10 getters, 2 runnings at 450 °C and 1 at room temperature, following which the gases were let into a MAP 215-50 mass spectrometer for measurement; the mass discrimination value was measured at 283 for $^{40}Ar/^{36}Ar$ (using a calibration noble gas mixture of known composition). System blanks were measured before and after every one or two sample analyses. Gas clean-up and inlet is fully automated, with measurement of ^{40}Ar, ^{39}Ar, ^{38}Ar, ^{37}Ar, and ^{36}Ar, each for ten scans, and the final measurements are extrapolations back to the inlet time.

The system blanks measured before and after every one or two sample analysis were subtracted from the raw sample data. Results were corrected for ^{37}Ar and ^{39}Ar decay, and neutron-induced interference reactions. The following correction factors were used: $(^{39}Ar/^{37}Ar)_{Ca} = 0.00065 \pm 0.00000325$, $(^{36}Ar/^{37}Ar)_{Ca} = 0.000265 \pm 0.000001325$, and $(^{40}Ar/^{39}Ar)_{K} = 0.0085 \pm 0.0000425$, based on analyses of Ca and K salts. Ages were calculated using the atmospheric $^{40}Ar/^{36}Ar$ ratio of 298.56 (Lee et al., 2006) and decay constants of Renne et al. (2011). All data corrections were carried out using an Excel macro and ages were calculated using Isoplot 4.15 (Ludwig, 2012). All ages are reported at the 2σ level and include a 0.5% error on the J value. Plateau criterium of at least 50% of the ^{39}Ar release in at least 3 consecutive steps was used.

4.2. Palaeobotanical sampling and study

Palaeocarpological fossils were recovered following Martinetto (2001b) with minor modifications. Selected organic-rich sediment and palaeosol samples were collected from the Porto da Cruz sediments (UVC2 g), dried overnight at 60 °C, deflocculated with 3% H_2O_2, washed through a 300 μm sieve, and the remaining residue dried at 60 °C. Seed fossils were hand-picked under a binocular microscope (Zeiss Stereomicroscope Stemi sv 11). The fossils were then rinsed overnight in 40% HF to remove silicates attached to the surface. Subsequently, fossils were mounted on metal stubs with carbon film, gold sputtered, and their morphology and anatomy investigated using a scanning electron microscope (SEM: Jeol JSM-5200LV). Identification of fossil seeds followed several atlas and books (e.g. Martin and Barkley, 1961; Kirkbride et al., 2006; Bojnanský and Fargašová, 2007; Cappers and Bekker, 2013), and palaeocarpofloras (e.g. Friis, 1985; Martinetto, 2001a; Czaja, 2003; Zhu et al., 2016). Fossil description followed the work by Friis (1985) and Zhu et al. (2016). Systematic taxonomy follows the criteria of Menezes de Sequeira et al. (2012). All seed fossils are numbered and deposited in the palaeobotanical collection within the Madeira University herbarium (UMad-P).

5. Results

5.1. $^{40}Ar/^{39}Ar$ geochronology

The UVC2 μ mugearite (sample nº 1) produced a plateau age of 1.319 ± 0.055 Ma, determined from steps 1–11 of the 12 steps, corresponding to 96% of the released ^{39}Ar (Fig. 3A). The inverse isochron plot (Fig. 3B) yields an age of 1.31 ± 0.23 Ma and the $^{40}Ar/^{36}Ar$ intercept is within error of an atmospheric ratio (298.56; Lee et al., 2006). The errors on the isochron calculation are larger than those of the plateau age. This results from the data points plotting on top of each other so that the spread along the isochron line is small, creating larger errors on the intercepts, particularly the $^{40}Ar/^{36}Ar$ intercept. For this reason, the plateau age is taken as the best estimate for the age of this sample.

The UVC2 basalt (*s.l.*) (sample nº 2) produced a plateau age of 1.38 ± 0.14 Ma which includes 74.2% of the released ^{39}Ar (steps 3–12 of 12; Fig. 3C). The inverse isochron does not provide much useful additional data due to the fact that all points plot very close together, so there is little spread along the line and very large errors on the intercepts (Fig. 3D). The larger errors on this sample compared to sample nº 1 may be, at least partially, related to the higher $^{37}ArCa/^{39}ArK$ ratio. In sample 2, this increases through the step-heating experiment, reaching 11 in the final step while in sample 1 the ratio is much more constant at about 2; this is usually a function of the sample chemistry.

Based on the data, the best estimates of the ages of these samples are the plateau ages: UVC2 μ mugearite: 1.319 ± 0.055 Ma, and the UVC2 basalt (*s.l.*): 1.38 ± 0.14 Ma. The obtained ages indicate that the Porto da Cruz sediments and respective fossil content are ~1.3 My-old, that is, Calabrian in age.

5.2. Palaeobotanical results

Fourteen specimens were recovered and studied. These are composed by complete, incomplete, and fragmentary seed fossils (Fig. 4), preserved as incarbonizations.

5.2.1. Systematic Palaeobotany

Division **Spermatophyta** Willk., 1854
Subdivision **Magnoliophytina** Frohne & U.Jensen ex Reveal, 1995
Class **Magnoliopsida** Brongn., 1843
Order **Theales** Lindl. 1833
Family **Theaceae** Mirb. ex Ker Gawl. 1816
Genus ***Eurya*** Thunb. 1783
†***Eurya stigmosa*** (R.Ludw.) Mai, 1960

Material: UMad-P180 (Fig. 4A); UMad-P181 (Fig. 4D; 5D); UMad-P182 (Fig. 4E); UMad-P183 (Fig. 4G); UMad-P184; UMad-P185; UMad-P186 (Figs. 4I and 5E); UMad-P187; UMad-P188; UMad-P189 (Fig. 4H); UMad-P190 (Fig. 4C); UMad-P191; UMad-P282 (Figs. 4F and 5A and G); UMad-P380 (Figs. 4C and 5B and F).

Description: Fossil seeds campylotropous, ranging from 1.04-0.81 to 1.74–1.3 mm in size, elliptical to angular in shape (Fig. 4A–H) and laterally compressed (Fig. 5A). External surface reticulated (e.g. Fig. 4A–B, F, G-I), formed by polygonal funnel-shaped cells, due to the narrowing of cell lumina towards the base (Fig. 5E–G). Surface cells are concentrically arranged around the condyle region in rows of 8–11 cells, with each cell 0.03–0.14 mm in diameter (average 0.10 mm). External funnel shaped cells in the condyle region circular (Fig. 5F) to elongated in shape. Funnel-shaped cells periclinal and anticlinal walls finely pitted (Fig. 5F-G). Seeds composed of two valves (Fig. 4G and H),

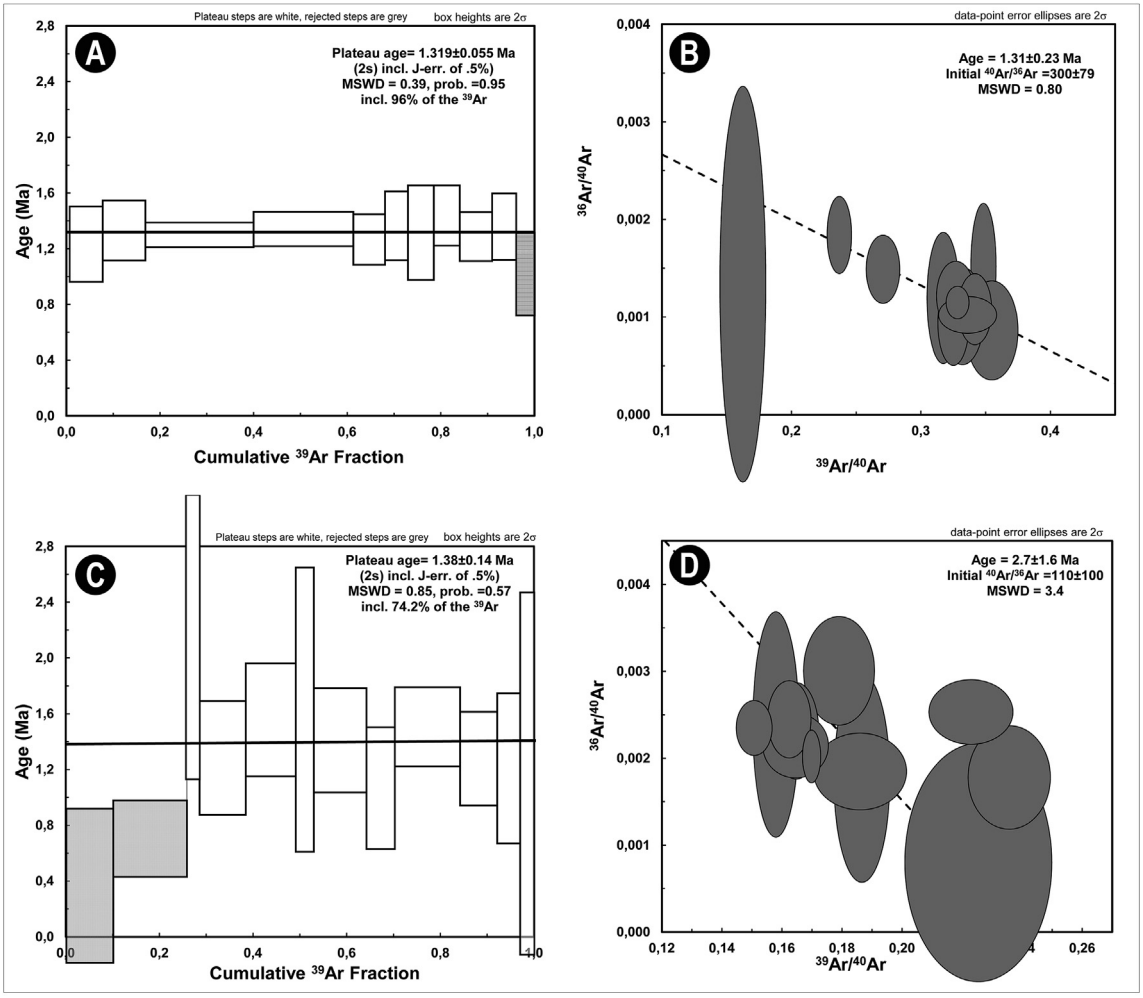

Fig. 3. Geochronology results from the $^{40}Ar/^{39}Ar$ dating. **A**, sample 1 (UVC2 μ) step-heating release spectra; **B**, UVC2 μ inverse isochron correlation plot; **C**, sample 2 (UVC2) step-heating release spectra; **D**, UVC2 inverse isochron correlation plot.

that split, revealing internally a horse-shoe shaped embryo cavity around the condyle region (Fig. 4D and E). Condyle is an inverted V shape, extended up to the middle of the valve (Fig. 4D and E). On the base of the condyle there is a subtriangular raphe hollow, a hilum formed by the condyle wall and the exotesta (Fig. 4E), and the micropyle (Fig. 4E; 5 B). The testa ranges between 0.06 and 0.14 mm in thickness and is composed by three layers, externally by a thin tegmen, seldom preserved, although present in some specimens (Fig. 4C and I), the exotesta composed by funnel-shaped cells and the endotesta, poorly preserved (Fig. 5C and D).

Comparison: The seed morphology and anatomy of living and fossil *Eurya* spp. is currently well studied and documented (see Zhu et al., 2016, and references therein). Madeira *Eurya* seed fossils were compared with previously determined seeds from both extant and fossil records examined by light microscopy (LM), SEM, and drawings (Mai, 1960, 1971; Corner, 1976a; Boulter, 1980; Friis, 1985; Collinson, 1990; Martinetto et al., 1997, 2015; Meller, 1998; Martinetto, 2001a; Czaja, 2003; Shi et al., 2012; Huang et al., 2016; Zhu et al., 2016).

Madeiran seed fossils can be assigned to the genus *Eurya* due to the presence of key morphological and anatomical characters, such as campylotropous seed shape, the presence of a thick exotesta, formed by polygonal funnel-shaped cells, concentrically arranged around the condyle with fine pitting and similar internal morphology of the condyle, raphe and hilum as extant *Eurya* spp. seeds (Friis, 1985; Shi et al., 2012; Zhu et al., 2016). These characters are distinctive from other similar Theaceae seeds, such as *Adinandra* Jack, *Cleyera* Thunb. or *Freziera* Sw. ex Willd. (Corner, 1976a, b; Friis, 1985; Zhu et al., 2016). Moreover, Theaceae is present in Madeira and Canaries Islands with the sole species *Visnea mocanera* L.f. (Jardim and Menezes de Sequeira, 2008). Morphological and anatomical comparison of *Eurya* seed fossils with fruits and seeds of *V. mocanera* L.f. (herbarium material: UMad MS 6194), shows that *V. mocanera* is distinct from *Eurya* spp., as fruits are indehiscent, the seeds are larger (ca. 3 mm), ovate shaped, and are strongly wrapped inside of a woody ovary (as mentioned by Mai, 1971). Due to this, *Visnea* palaeocarpological remains are mainly represented by abraded fruits (by loss of fleshy perianth) and rarely by isolated seeds (e.g. Mai, 1971).

The identification as *Eurya stigmosa* is further supported by the comparation with the seed fossils descriptions given by Mai (1960), Friis (1985) and Zhu et al. (2016) with other 11 *Eurya* taxa based on seed fossils (Zhu et al., 2016: Table 2): Madeira seeds diameter (1.04–1.74 mm) falls within the average diameter of *E. stigmosa* (1–2.5 mm); Madeiran seeds shape variability is comparable; the funnel shaped cells medium diameter is the same (0.10 mm); testa thickness (0.06–0.14 mm) is similar (0.05–0.15 mm). Overall, the seed fossils found in Porto da Cruz sediments can be assigned to the

Fig. 4. SEM images of the external and internal morphology and variability of *Eurya stigmosa* (R.Ludw.) Mai seed testa fossils from the Porto da Cruz sediments (Madeira Island). **A,** UMad-P180, **F,** UMad-P380, and **I,** UMad-P282 showing the size and morphological variability; **B**, UMad-P182 and **C**, UMad-P181, internal views of the valve showing the campylotropous embryo cavity, where the hilum (H), micropyle (M), raphe (R), chalaza (Ch) and condyle (C) are visible; **D**, UMad-P190, still with tegmen (Tg) preserved; **E**, UMad-P186, fragment of a seed valve; **G**, UMad-P183 and **H**, UMad-P189, specimens still showing two valves (Va) attached together.

genus *Eurya* and to the extinct species *E. stigmosa* (R.Ludw.) Mai.

6. Discussion

6.1. Palaeobiogeographical implications

According to Min and Bartholomew (2007), the genus *Eurya* has 130 species, distributed through tropical and subtropical South and Central America, Western Asia and the Pacific Islands (Fig. 6A). However, the *Eurya* fossil record shows a different palaeobiogeographical distribution (Fig. 6A). Several fossils (mainly seeds), from the Cretaceous (Knobloch and Mai, 1986) to the Early Pleistocene (Martinetto et al., 2015; Chochieva, 1975 in Martinetto et al., 2017) were reported in Europe (Austria, Bulgaria, Czech Republic, Denmark, Germany, England, Italy and Poland), Russia, Japan and China (Zhu et al., 2016, Table 3, and references therein). Additionally, *Eurya* was also identified for the Oligocene of Ireland (Boulter, 1980) and Pliocene of Portugal (Vieira et al., 2011). In this context, the Madeiran specimens represent the westernmost fossil record of *Eurya* (Fig. 6). *E. stigmosa* was first recognised from the

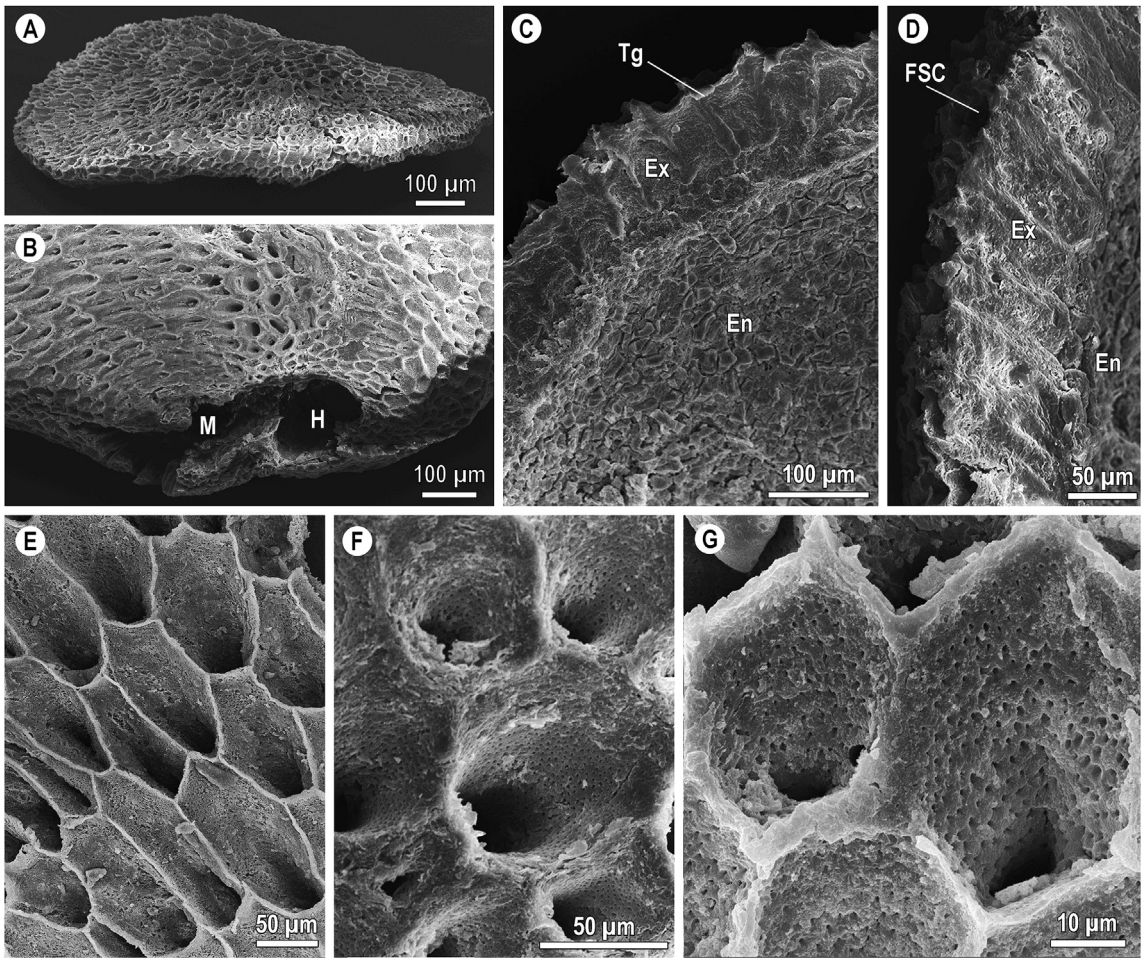

Fig. 5. SEM images of morphological and anatomical details of *Eurya stigmosa* (R.Ludw.) Mai. **A**, UMad-P282, lateral compressed aspect of the seeds; **B**, lateral view of the specimen UMad-P380 showing the micropyle (M) and hilum (H); **C,** UMad-P182 and **D**, UMad-P181, detail of the wall of the internal seed testa, with remains of the tegmen (Tg), exotesta cells (Ex), and endotesta (En) poorly preserved; **E**, UMad-P186, detail of the exotesta polygonal funnel-shaped cells; **F**, UMad-P380 and **G**, UMad-P282, detail of the funnel-shaped cells and the pitting.

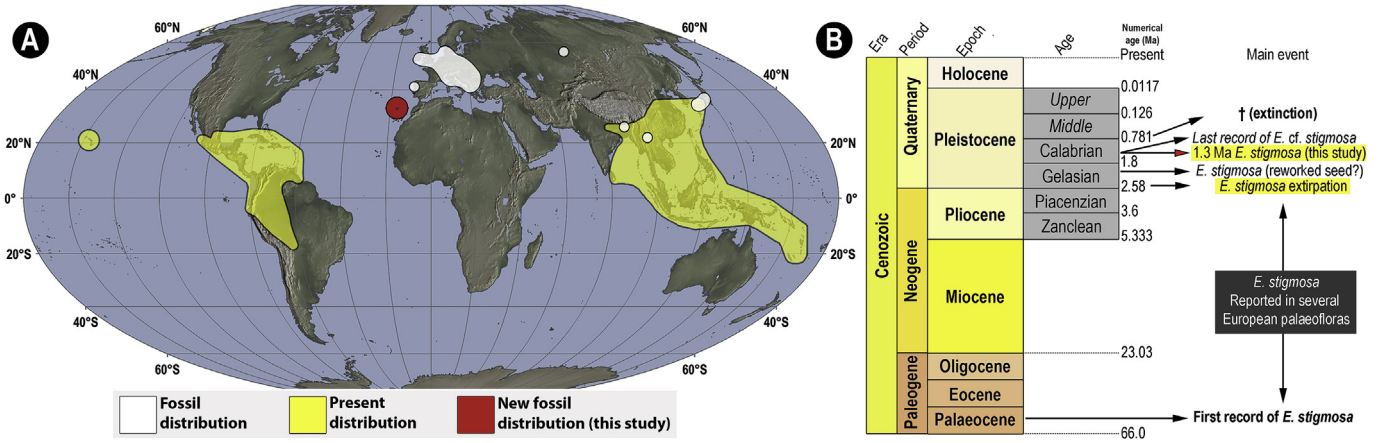

Fig. 6. *Eurya* spp. geographical range and geological history. **A**, Past (based on fossil record of the genus *Eurya*), present and new distribution of *Eurya* spp. (adapted from Knobloch and Mai, 1986; Zhu et al., 2016); **B**, Palaeobiogeographical history of *Eurya stigmosa* through the Cenozoic. Digital elevation models generated in GeoMapapp (http://www.geomapapp.org) using the global multi-resolution topography (Ryan et al., 2009).

Palaeocene of England (Mai, 1971), and it was a common element in Mio-Pliocene European palaeofloras (Zhu et al., 2016), becoming extirpated and extinct during the Pleistocene (Martinetto et al., 2015, 2017). In Northern Italy during the Pliocene-Pleistocene transition, *E. stigmosa* disappears together with several other thermophilous plant taxa (Martinetto et al., 2017). In Europe, the

last record of *E. stigmosa* is known from the Gelasian of Italy, from a single seed, possibly reworked (Martinetto et al., 2015) and by a second record, identified as *E.* cf. *stigmosa*, from the Calabrian of Georgia (Chochieva, 1975 in Martinetto et al., 2017). These Early Pleistocene records are interpreted as populations in a refugium situation due to Pleistocene glaciations (Martinetto et al., 2017). Thus, Madeiran *E. stigmosa* new record and 1.3 Ma age also represents a Calabrian population in refugium and one of the last fossil records for the species (Fig. 6B).

From an oceanic island biogeographical point of view, the identification of *E. stigmosa* in Madeira is further proof to support the Macaronesian islands (Azores, Canaries, Cabo Verde and Madeira) as repositories for several plant taxa that were widespread in the European palaeotropical geoflora (Mai, 1991), such as Lauraceae (e.g. *Ocotea* Aubl., *Persea* Mill.), Theaceae (*Visnea* L.f.), Sapotaceae (*Sideroxylon* L.), Clethraceae (*Clethra* L.) (e.g. Heer, 1857; Williamson, 1984; Mai, 1991; Press and Short, 1994; Fernández-Palacios et al., 2011; Martinetto et al., 2017; Vieira et al., 2018). The arrival of *E. stigmosa* into Madeira was certainly facilitated from continental source by stepping-stone, through palaeo-Macaronesian Islands that existed since at least the last 27 Ma, possibly 60 Ma (Fernández-Palacios et al., 2011).

The key question is how did *E. stigmosa* became extinct in Madeira? This species has ecological requirements and a biogeographical history shared with many plant taxa still present in Madeiran flora (see Martinetto et al., 2017). A broad biogeographical explanation can be found within the GDM (Whittaker et al., 2008; Borregaard et al., 2017). The model forecasts that the number of extinct (and extirpated) species increases as an island starts to subside, due to the loss of carrying capacity (K), which reflects on area and habitat loss. Looking at Madeira Island topography, it corresponds to a deeply carved volcanic edifice that is subsiding over the last ~5.6 My (Ramalho et al., 2015). This means that, although it still presents relatively high topographic complexity, cumulative subsidence through geological time allied with erosion must have contributed to area loss and, consequently, habitat loss.

However, stricter biogeographical explanations are needed to clarify this disappearance. Fernández-Palacios et al. (2016) presented the GSM, in which island extinctions were reportedly caused by Pleistocene glaciations. This includes a list of theoretically and empirically based predictions on how islands and respective biota could be shaped by climate change and eustatic movements in a glacial and interglacial period. One of the predictions is that an island's fossil record would, eventually, reveal the presence of natural extinct taxa due to area change and eustatic movements (Fernández-Palacios et al., 2016: Box 1).

The GDM predictions, coupled with GSM impacts of Pleistocene glaciations such as climate change and islands area reduction/expansion on Madeira Island, most probably had a significant contribution to the extinction of *E. stigmosa*. Furthermore, other geological factors probably contributed such as recurrent volcanism that capped the island during the UVC and mega-landslides able to remove large portions of an island and the biota within (Brum da Silveira et al., 2010a; Quartau et al., 2018).

6.2. Palaeoecological implications

To fully understand the extinction of *E. stigmosa* in Madeira, a palaeoecological perspective is needed. In mainland Europe, Martinetto et al. (2017) propose that *E. stigmosa* extirpation and extinction along with several other thermophilous taxa were driven by the lack of autecological adaptations to the Pleistocene glacial and interglacial cycles. Based on Italian palaeocarpological taxa and the present distribution of the same generic or infrageneric taxa Martinetto et al. (2017) proposes three main plant categories that were growing together in the European late Cenozoic: HUTEA (standing for 'humid thermophilous taxa of East Asian affinity') that do not tolerate a mean annual temperature (MAT) below 8 °C and mean annual precipitation (MAP) below 800–1000 mm/year; a second, CTEA (Cool-Tolerant extinct European taxa of East Asian affinity) that tolerate a MAT < 8 °C; and a third, coined TEWA (Thermophilous European, West Asian and/or African elements), that do not tolerate a MAT < 8°, but tolerate aridity and is found in southern Europe, North Africa and Macaronesia. *E. stigmosa* falls within the CTEA group with a 5.5 °C MAT (see Table 1 in Martinetto et al., 2017). Comparing MAT and MAP proposed for *E. stigmosa* with present Madeira MAT and MAP, Madeira could not only have *E. stigmosa* still growing, but also all the groups proposed by Martinetto et al. (2017). Madeira MAT and MAP are a function of the topography, and the influence of trade winds in the windward and leeward areas of the Island. In leeward coastal areas (e.g. Funchal, Lugar de Baixo), the MAT varies between 19 and 19.7 °C and MAP ~600 mm (Barceló and Nunes, 2012), and in central higher altitudes (e.g. Bica da Cana at 1560 m a.s.l) MAT can reach 6-12 °C and MAP >2600 mm (Barceló and Nunes, 2012). Moreover, the climate of Madeira Island allows the presence between ca. 300–1450 m a.s.l. (leeward face) and 50–1400 m a.s.l (windward face) of two vegetation belts of evergreen broad-leaved trees dominated by Lauraceae, the barbusano-tree Mediterranean forest series (*Semele androgynae-Apollonio barbujanae* sigmetum) and the stink-laurel temperate forest series (*Clethro arboreae-Ocoteo foetentis* sigmetum) (Capelo et al., 2004, 2005). It is plausible that *E. stigmosa* in Madeira occurred within these types of vegetation, as today *V. mocanera* occurs within the barbusano-tree forest (Capelo et al., 2004, 2005). Furthermore, the stink-laurel temperate forest already existed 1.8 My ago on Madeira Island (Góis-Marques et al., 2018). Extant *Eurya* spp. are evergreen dioicous shrubs and small trees, rarely trees (Min and Bartholomew, 2007). Present *Eurya* spp. species grow today in Japan and China as understory shrubs in the evergreen broad-leaved forest community (Wang et al., 2007; Manabe and Yamamoto, 2009). The existence of *E. stigmosa* at least until the Calabrian in Madeira could also be explained by less severe climate during the early Pleistocene glaciations (when compared to Europe), due to the lower latitude and oceanic characteristics, allowing the maintenance of a warm buffered climate. This could have delayed the extirpation until the glacial cycles became more extreme by the late Pleistocene.

Today, the only living Theaceae in Madeira, *V. mocanera,* is a rare tree, confined to the deep gorges or steep cliffs on the north coast (Whitefoord, 1994). This is most probably due to anthropogenic impacts since the human settlement of the island in 1419. This leads to further ask: could *E. stigmosa* have survived the Pleistocene glaciations until the early Portuguese settlement? If so, could this be a case of a pre-Linnaean extinction of a palaeoendemism (Jardim and Menezes de Sequeira, 2008)? Finally, although very unlikely, could *E. stigmosa* still be growing in the Madeira archipelago unnoticed in some inaccessible steep ravines?

7. Conclusions

Based on the identification of *E. stigmosa* fossils on Madeira Island, its palaeobiogeography, palaeoecology, and new geochronology dating of Porto da Cruz sediments, we can provide several conclusions. The new ^{40}Ar-^{39}Ar geochronologic dating allows us to constrain the age of the Porto da Cruz sediments to ~1.3 Ma (Calabrian) in age. From these sediments, especially layer 2 (Fig. 2B), it was possible to retrieve seed and fruit fossils. Among these, 14 *Eurya* sp. fossil seeds were recovered. Based on morphological and anatomical characters observed from light microscopy and scanning electron microscopy, it is possible to determine the

seeds as belonging to the extinct taxon *E. stigmosa* (R.Ludw.) Mai. These results expand the palaeobiogeography of this species to the Mid-Atlantic, and into the Macaronesian realm. *E. stigmosa* is the first extinct plant identified from the Madeira island fossil record. Moreover, this record is the first extinct plant species found as a fossil on an oceanic island, as previous identifications are most probably extirpations or taxonomical misinterpretations. The new ^{40}Ar-^{39}Ar and palaeobiogeographical data makes the new identification of Madeiran *E. stigmosa* one of the last records of *E. stigmosa* worldwide, which was already in a refugium situation. The extirpation of *E. stigmosa* in Madeira is most probably due to natural events, like island ontogeny (e.g. subsidence, volcanism) and Pleistocene glaciations as predicted by the GDM and GSM models. The delayed disappearance, when compared with continental records, is most probably related to an island refugium from the severe continental Pleistocene glaciations, allowing the survival of *E. stigmosa* until the Calabrian. From the Calabrian onwards, the species disappearance from Madeira could be related to species palaeoautecology and the inability to cope with the deteriorating Pleistocene glaciated climate, that was eventually reflected in Madeira Island palaeoclimate. Although unlikely, we can't rule out its survival into the Holocene, and an anthropogenic driven extinction related with the 15th century Portuguese settlement of Madeira Island.

As concluding remarks, we wish to point out the importance of palaeobotanical studies on oceanic islands worldwide, with a special focus to palaeocarpological studies, that allows the identification to species level (Martinetto et al., 2017). As a last thought, the identification of this extinct species can be a prelude to the discovery of other extinct plant taxa in Madeira and other Macaronesian islands, so we ask, are there other CTEA and HUTEA (sensu Martinetto et al., 2017) extinctions in Macaronesia? This question should also be reformulated and addressed to all oceanic islands worldwide: are there any extinct or extirpated plant fossils within their geological record?

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